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A REVIEW OF THE BIOLOGY OF SEX-DETERMINATION¹

SIDNEY I. KORNHAUSER

1. PREVALENT IDEAS

The mechanism of sex-determination has been a matter of speculation since time immemorial. Many erroneous and impossible ideas remain even today in the mind of the layman. The speculations may be gathered in three groups according to whether belief is held (1) that the sex of the offspring is pre-determined in the egg, (2) that sex is determined at the time of fertilization, or (3) that sex is not determined until after the zygote has been formed.

All of the older experiments on sex-determination were based on the third supposition. It was believed that by varying the nutrition of the developing embryo one sex or the opposite would result. This belief was even applied to human beings. In experiments upon tadpoles definite results were believed to have been attained, but we now know that the death rate in these experiments was so large that the results may be explained by a differential mortality.

Others held that the age or vigor of the parent affected the sex ratio, the older or the more vigorous of the two parents tending to impress its sex upon the offspring.

Another belief, and one still held by many, regards the freshness or staleness of the egg as important. An egg shortly after ovulation tends to produce a female, while an egg which has remained in the oviduct some time would tend to produce a male.

The idea that two types of eggs are formed is not altogether new. Thus, entirely without biological foundation, theories

¹ A lecture delivered before the Denison Scientific Association in October, 1921.

were propounded that one ovary gave rise to male-producing eggs whereas the opposite ovary gave rise to female-producing eggs. Equally valid was the theory that one testis gave rise to male-determining spermatozoa and the opposite testis gave rise to the female-producing spermatozoa. Two sorts of eggs in equal numbers and one type of sperm would give a 50:50 ratio; also two sorts of sperm in equal numbers and one type of egg would give a 50:50 ratio.

These latter ideas are found in modern theories of sex-determination, but today they are based on an actual biological foundation through the use of the microscope and breeding tests.

2. CHROMOSOMES AND SEX

Modern theories of sex-determination hold to the first and second propositions, stated in the first paragraph of this article. If there are two kinds of eggs, male determining and female determining, then the sex of the individual is already fixed before the sperm nucleus has united with the egg nucleus. At least we may say that with the extrusion of the polar cells, the mechanism has been brought into play. If there are two kinds of sperm, male determining and female determining, then sex-determination depends on the type of sperm uniting with the matured ovum, and we may say that sex is determined at the time of fertilization.

Our present day stand on these questions is based entirely on direct observation, both cytological and experimental. In 1902, McClung discovered an unpaired chromosome in the testes of certain Orthoptera and this chromosome he called a sex-determiner. This observation, together with the association of this chromatic body with sex-determination, was of primary importance and it opened up a new era in cytological work. Volumes have been written on the mechanism of sex-determination since 1902, and even at the present time facts on this subject are being added almost daily.

In many groups of animals there is an unpaired chromosome in the male, which is called the X-chromosome. This can be seen in the somatic cells, in the spermatogonia and in the sperma-

toocytes (fig. 1). We now know that the X-chromosome is paired in the female cells, both somatic and germinal. In

Diploid Group, Male

Diploid Group, Female

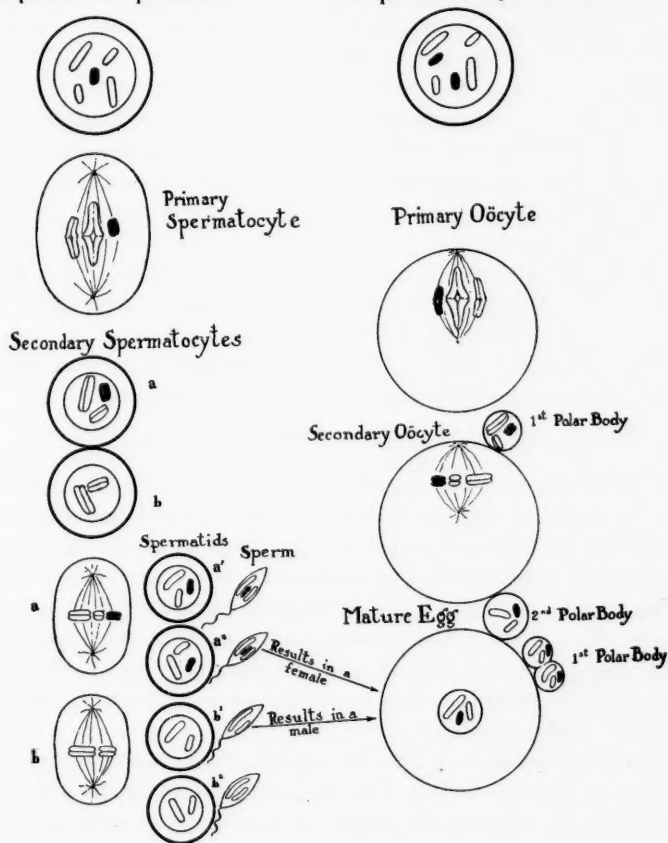


FIG. 1. SIMPLEST KNOWN MECHANISM OF SEX-DETERMINATION

The X-chromosome is shown as black; the autosomes are in outline

spermatogenesis the autosomes pair to form tetrads. In the first spermatocyte division the tetrads are reduced to dyads and the X-chromosome generally passes undivided to one second

spermatocyte. In dividing again into spermatids, this second spermatocyte (fig. 1, a) gives rise to X-bearing cells which form the female-determining spermatozoa. The sister second spermatocyte which did not receive an X-chromosome gives rise to the two male-determining spermatozoa. A zygote which receives two sets of autosomes and two X-chromosomes is a female; a zygote which receives two sets of autosomes and one X-chromosome is a male. Since in general both types of sperm are formed in equal numbers, the chances of a male- or female-determining spermatozoan reaching the egg in the process of fertilization are equal, and in general 50 per cent of the resulting zygotes are male and 50 per cent female.

The foregoing case is the simplest mechanism known. While this is a fundamental type, still there are many variations of the mechanism. Thus the X-chromosome may have a Y partner in the male cells. If n = one set of autosomes in a given animal, then we have the following combination in this case:

$$2n + XY = \text{male, and } 2n + 2X = \text{female}$$

In the spermatogenesis of such animals, two spermatids receive an X-chromosome and two a Y-chromosome, the latter being the male-determining spermatozoa. In other cases the X-chromosome may be represented by several discrete components; and it may or may not have a Y-chromosome associated with it in the male cells. Thus in *Gelastocoris*, an hemipteron, the male is represented by $2n + 4X + Y$ and the female by $2n + 8X$. " n " here equals fifteen, so the male diploid number is 35, and the female diploid number is 38.

Detailed studies of the sex chromosomes have brought out many interesting facts. The X-chromosome in some animals is attached to a certain autosome, as in *Culex* or in *Ascaris megalocephala*. When paired, as in the female somatic cells or in oöcytes, the X-chromosomes behave similarly to autosomes in mitosis and in the mitotic divisions and also in syndesis. Contrary to this, the unpaired X-chromosome of the male acts rather unlike an autosome in the spermatocytes. It fails to form a leptotene thread, generally appearing as a conspicuous karyo-

some. Very often it lags behind the anaphase autosomes in either the first or second spermatocyte division. The Y-chromosome likewise often fails to form a leptotene thread. In the growth of the spermatocyte, and in the maturation divisions, the X- and Y-chromosomes show considerable variation in degree of association. In the primary spermatocyte division of many Heteroptera the X- and Y-chromosomes divide independently. They then come into contact and separate reductionally in the second spermatocyte division.

We may now ask how the sex chromosomes are related to the autosomes. That the X-chromosome bears many genes for characters having nothing to do with the process of sex is known from breeding experiments. In the female the X-chromosomes, except where there are differences in size, cannot be distinguished from ordinary autosomes. Recent experiments, especially those of Bridges on *Drosophila*, indicate very clearly that there are specific sex-genes in the X-chromosome, which working in conjunction with the genes of the autosomes are capable of producing males or females or even intermediates in cases where the normal relationship is upset.

We are therefore entirely rid of the older idea that the X-chromosome is composed of a different kind of chromatin from that found in the autosomes and that the sex of the zygote depends upon the amount of X-chromatin it receives. Sex is now put upon a basis of specific genes.

The Y-chromosome until recently has not been known to carry specific genes for bodily characters. Indeed, this chromosome is generally regarded as merely a degenerate X-chromosome which has lost its sex-genes and most of its other genes as well. That it is essential to normal development in species ordinarily having it present was shown in the non-disjunction experiments of Bridges. Thus, male *Drosophila* without a Y-chromosome are sterile. In size the Y-chromosome may be as large as the X or it may be almost insignificant in comparison to it. In *Enchenopa binotata*, studied by the author, both the X and Y elements form threads in the leptotene stage of the primary spermatocytes. These threads are thicker than those of the autosomes and never

conjugate laterally, remaining in contact merely at one end. They are not widely removed from the autosomes in their activities and staining powers in the species. However, in other forms, such as *Anisolabis*, studied by the author, the Y-chromosomes may exhibit entirely different staining reactions from the X-chromosome. It may be looked upon as degenerate from a cytological standpoint.

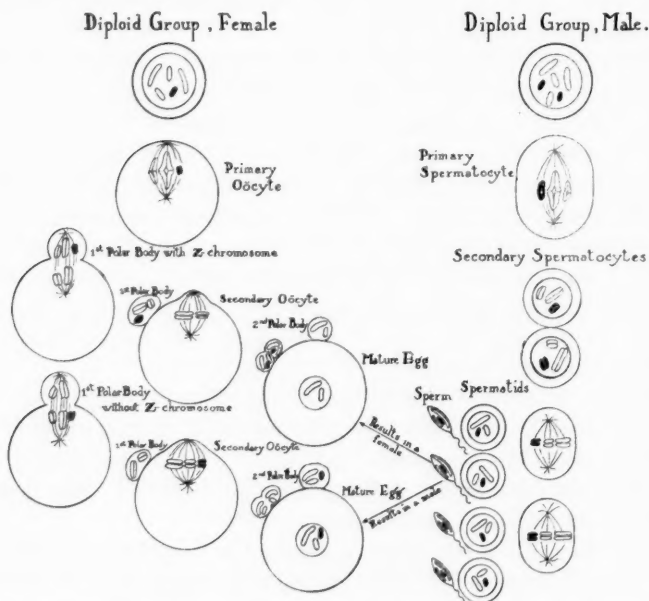


FIG. 2. MECHANISM OF SEX-DETERMINATION IN WHICH TWO TYPES OF OVA ARE PRODUCED

The Z-chromosome is shown in solid black

In many forms it is therefore not unlikely that, although there is no sex-determining mechanism visible to us with the aid of our best microscopes, nevertheless X and Y chromosomes exist, the Y-chromosomes being practically equal in size to the X-chromosomes and differing from them merely in the absence of specific genes.

The reverse of the foregoing mechanism described for insects and mammals is to be found in the Lepidoptera and the birds. In these groups the presence of $2n + 2X$ or $2Z$ (as the sex-chromosomes are here called) results in a male and $2n + X$ or Z produces a female. These facts are well borne out by breeding experiments in both groups. The cytological basis is not so strong, for both avian and lepidopteran chromosomes are rather difficult to study.

In the moths definite results have been reached by Seiler and also by Doncaster, showing that two types of ova are produced. Those which extrude the Z-chromosome in the polar cell will when fertilized produce females, those which retain the Z-chromosome when fertilized will produce males.

It is obvious from the diagram, figure 2, that the sex of the zygote depends entirely upon the maturation of the ovum, the retention or expulsion of the Z-chromosome being the deciding factor. If in any way maturation can be controlled by factors exerting their influence either from within the egg itself or external to the egg, then sex ratios may be altered from the normal 50:50. Seiler has done this in the case of moths by varying the temperature. It also offers a possible explanation of such sex ratios as have been obtained by Riddle in his forced breeding experiments of doves, where females are produced in the latter part of the season from larger eggs and males in the early part of the season from smaller eggs.

3. COMPLICATED LIFE CYCLES

The most enlightening observations on the determination of sex through maturation are those in the aphids and phylloxerans studied by Morgan and von Baehr. Let us examine the case of *Aphis saliceti* of von Baehr. It is well known in these insects that fertilized eggs always produce females. During unfavorable conditions both males and females are produced by parthenogenesis, the males, however, always arising from smaller eggs. It has been shown that in these small eggs (represented at the extreme right in figure 3) a whole X-chromosome is extruded in

the formation of the one polar cell, leaving in the egg $2n + X$ chromosomes (five in number), and that such an egg forms a male. In the larger parthenogenetic eggs no whole X-chromosome is extruded in the single polar egg given off, and the egg retains $2n + 2X$ chromosomes (six in number) and develops into a female. In the spermatogenesis of these forms it was found that only one secondary spermatocyte develops, that which received the X-chromosome. Thus only two instead of four spermatids result from a primary spermatocyte and these are

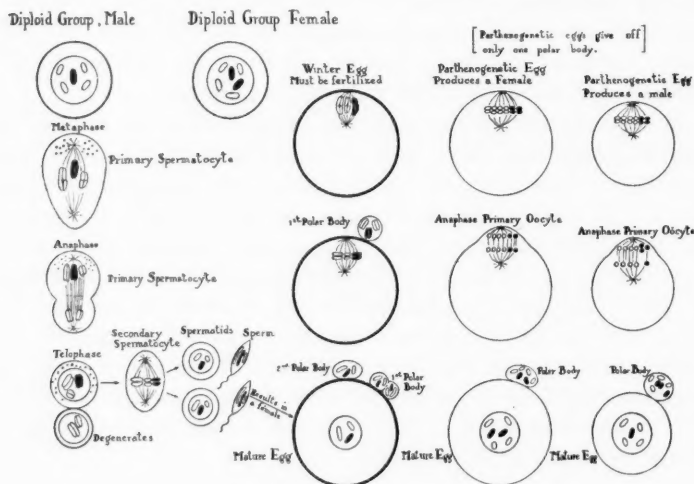


FIG. 3. SCHEME OF REPRODUCTION OF APHIDS AND PHYLLOXERANS

female-determining spermatozoa. In this case of the phylloxerans and aphids it would thus appear that maturation is in reality controlled by the size or composition of the egg.

It is rather unfortunate that the rotifers and daphnids are not such favorable cytological material as the homopterans for it is not at all unlikely that their sexual cycles rest upon a basis similar to that above described. In rotifers and daphnids the biological conditions are almost identical with those of the aphids and phylloxerans. Fertilized eggs give rise only to females,

whereas parthenogenesis may result either in females or males, the latter coming from smaller eggs. This is all the more interesting because both Whitney and Shull, working on rotifers, have by external conditions been able to alter the normal cycle and to cause the discontinuance of parthenogenesis, thus bringing on the production of male individuals and eggs which require fertilization. They have evidently through these conditions influenced the type of egg produced. The type of egg would then control its own maturation if the case were parallel to that of Aphis and Phylloxera.

In the Cladocerans, where parthenogenesis alternates with a sexual cycle and at least three kinds of eggs are produced (thick shelled, fat laden, ephippial eggs which must be fertilized; thin shelled, glycogen laden, parthenogenetic eggs, developing into females; and thin shelled, smaller parthenogenetic eggs, developing into males), the type of egg produced may be influenced by temperature and food, as was shown by Geoffrey Smith. It is not improbable that we may yet see in the maturation of these ova differences in chromosomal behavior correlated with each type of ovum and the sex of the resulting offspring.

Closely allied to the foregoing problem is the question of sex determination in the Hymenoptera. Even before chromosomes were known, Dzierzon postulated that males (drones) were formed from unfertilized eggs and females (workers and queens) from fertilized eggs. This has been substantiated nicely, both from cytological and genetical investigation. Newell showed in bee matings of Italian (grey) queens and German (dark) drones, and also in reciprocal crosses, that the male offspring of such matings were purely maternal while the females were hybrid in character. Cytological observations by Petrunkevitch and Nachtsheim have also established the validity of the Dzierzon theory. Coupled with this, observations on the spermatogenesis of Hymenoptera have revealed interesting results. The spermatogonia possess merely the haploid number of chromosomes. In order that this number be not further reduced in the process of spermatogenesis only one division of the chromatin takes place. In the bee the first spermatocyte division results in all the chromatin passing

to one centrosome; a minute degenerate non-chromatic globule is formed at the other pole of the spindle. In the second maturation division, the chromatin divides, but one of the spermatids is very small and degenerates. Thus only one instead of four spermatids is formed, and it contains the haploid number of chromosomes. Variations of this process are found in other Hymenoptera, resulting frequently in two spermatids from the larger second spermatocyte, each possessing the haploid number of chromosomes.

The possibilities of sex production through parthenogenesis are many. Reduction to the haploid number, or the elimination of a whole X-chromosome, may produce a male, whereas the elimination of one maturation division may allow the egg to retain the diploid number and develop into a female. Still further possibilities are offered in cases where either the retention of the Z-chromosome or its elimination is of vital concern in the resulting offspring. Goldschmidt has reared both sexes from unfertilized moth eggs.

4. POLYEMBRYONY

Closely allied to the subject of the chromosomal basis of sex are the facts of polyembryony. Where more individuals than one are formed from an ovum they are almost invariably of the same sex. The classical examples are parasitic Hymenoptera, principally of the families Proctotrypidae and Chalcididae, where often thousands of individuals result from a single egg. Other examples are the quadruplets formed in the nine-banded armadillo, and identical or monochorial twins in man and other mammals. In the case of mammals the type of sperm (either with or without an X-chromosome) is undoubtedly the deciding factor. Providing then that all the chromosomes of the zygote divide normally, the sex of the resulting individuals must be the same, and they will be genetically identical. In the Hymenoptera the sex will depend entirely on fertilization or parthenogenesis. A fertilized egg will result in females and an unfertilized ovum in males. Patterson has occasionally got one or a few males in a

female brood, but these he explains on the basis of an imperfect mitosis, resulting probably in the loss of a specific chromosome which probably bore the sex-determining genes. This supposition is based on direct cytological observation. The facts of polyembryony offer a strong substantiation to the idea of chromosomal determination of sex.

5. SEX-LINKED INHERITANCE

The association of Mendelian characteristics with particular chromosomes is nowhere better shown than in the group of the sex-linked characteristics. The genes for these characteristics, of which alone thirty odd are known for *Drosophila*, are undoubtedly located in the sex chromosomes, and their inheritance follows the distribution of these chromosomes exactly.

Let us take for example the inheritance of red eye in *Drosophila*, a dominant sex-linked characteristic (see fig. 4). If a red eyed female is mated to a white eyed male, the F^1 are all red eyed. If the F^1 are again inbred, the F^2 generation are three red eyed to one white eyed, but the peculiar thing is that all the white eyed individuals are males. Thus, half the F^2 males are like their grandfathers. White-eyedness is covered up when the gene for red is present, and this is the case in all the F^1 females. However, the eggs of the F^1 female, which eliminate the red gene in the polar body in maturation and are then fertilized with a sperm bearing a Y-chromosome, will result in white eyed offspring. Thus we can say that the males have inherited their white eyes from their mothers through the X-chromosomes which she contributed to the zygotes.

Let us now examine the cross reciprocal to that given first. As shown in figure 5, we get an entirely different result. The F^1 females are red eyed like their fathers, and the males are white eyed like their mothers. In the F^2 generation half the males and half the females are white eyed and the others red eyed. This result is due to the fact that the male has a mechanism (only one X-chromosome) capable of bearing the gene for red but once. This is a cross therefore of a heterozygous dominant

male (red eyed) back to a recessive female (white eyed) and gives a 1:1 ratio. The F^1 females (which must have two \underline{X} -chromosomes) all received an \underline{X} -chromosome from their father and are red eyed. The F^1 males all received their single \underline{X} -chromosome from their mothers and are white eyed.

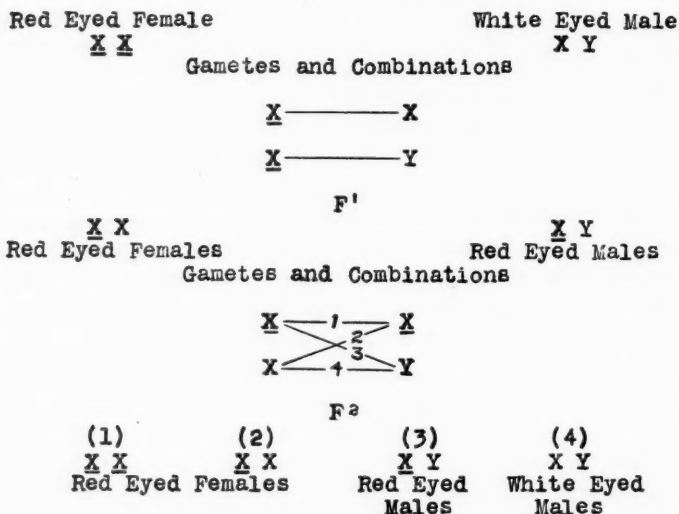


FIG. 4. DIAGRAM SHOWING SEX-LINKED INHERITANCE IN *DROSOPHILA*

An underscored \underline{X} represents an X-chromosome bearing the gene for red eye; because this is dominant over white eye, any individual with an underscored \underline{X} will have red eyes.

This criss-cross type of inheritance has long been known in man. Color-blindness is perhaps the best known illustration and behaves in its inheritance exactly like red eye in *Drosophila*. That color-blind females are so rare is due to the fact that normal color vision is dominant over color-blindness, thus \underline{XX} and \underline{XX} are females with normal color vision; but the latter is a carrier for color-blindness. \underline{XY} is a normal male and XY a color-blind male. The mating of a female carrier with a color-

blind male would result in the production of 50 per cent color-blind females as shown in the diagram, figure 6.

In animals in which the female is heterogametic (Lepidoptera and birds) sex-linked characteristics are likewise known to exist. In fact the first sex-linked characteristics were discovered in moths by Doncaster. In these cases it is the female which possesses the mechanism whereby the character in question can only be present once. Let us take, for example, barring, a

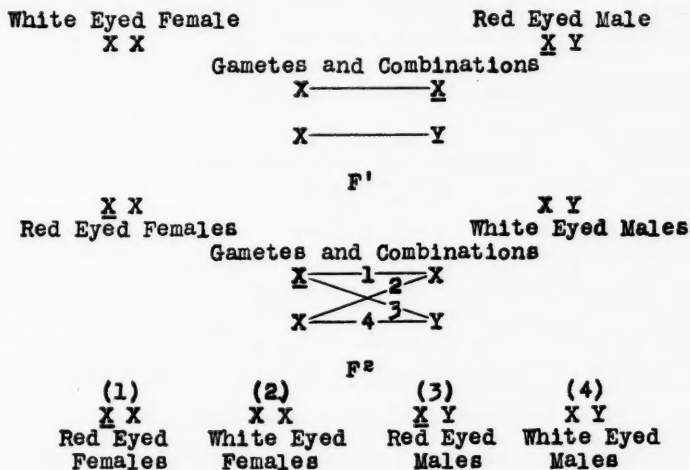


FIG. 5. DIAGRAM SHOWING CROSS RECIPROCAL TO THAT SHOWN IN FIGURE 4

dominant sex-linked trait in poultry. As shown in figure 7, the F² generation results in three barred to one black, but the black individuals are all females.

The reciprocal cross likewise shows that the character for barring follows the distribution of the Z-chromosome. As indicated in figure 8, the F¹ males are barred because they got a Z-chromosome from their maternal side; the F¹ females are black because their lone Z-chromosome came from the paternal side.

6. SECONDARY SEXUAL CHARACTERISTICS AND HORMONES

The primary difference between the sexes is in the formation of gametes. The female is an egg producer, the male a sperm producer. In many animals, especially invertebrates, it is very difficult to distinguish males from females without first examining the gonads. On the other hand there is no lack of forms in which one can with ease distinguish the sexes by external appearances. Sometimes this sexual dimorphism extends to all parts of the organism. Compare the minute male of *Bonellia* with the female, hundreds of times its size, for example.

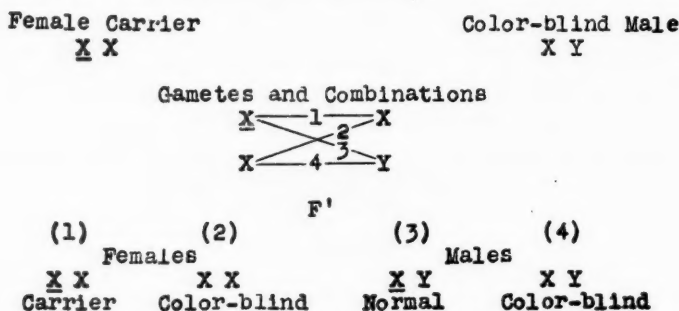


FIG. 6. DIAGRAM SHOWING SEX-LINKED INHERITANCE IN MAN

An underscored X indicates the presence of the gene for normal color vision; because this is dominant over its allelomorph, color-blindness, any individual with an underscored X has normal color vision.

Very often, however, the dimorphism is confined, first, to the genitalia or to accessory apparatus used in copulation, oviposition or rearing of the young, and, second, to extragenital characteristics not associated directly with reproduction, color and ornaments and the like. Both of these classes are, however, secondary to gamete production. In mammals and birds these so called secondary sexual characteristics are found to be largely dependent for their proper development on the normal presence and activity of the gonad. The castration of young male mammals results in individuals lacking in many ways the attributes

of normal males. In cattle and horses the individuals are docile compared with the fiery males. They lack the thick neck and put on fat more readily than males. In man, the voice fails to change, the epiphyses of the bones fail to fuse, the beard is weak, and the spirit dulled. Females deprived of ovaries early in life fail to develop normal mammary glands, and the skeletal characteristics likewise are much altered. Extensive experiments have proved that in birds and mammals secretions

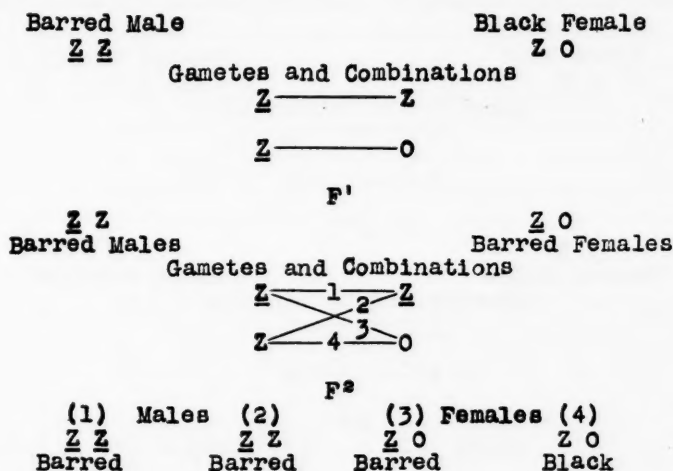


FIG. 7. DIAGRAM SHOWING SEX-LINKED INHERITANCE IN POULTRY

An underscored \underline{Z} indicates the presence of the gene for barring; because this is a dominant gene, any individual with an underscored \underline{Z} will be barred.

of the gonads are essential to normal development. The castration of young male rats followed by the ingrafting of ovaries causes these individuals to be feminized. They develop mammary glands, have female characteristics of skeleton and hair pattern, and also possess female sexual instincts.

Perhaps no better case of hormone influence is known than that of the freemartin, adequately explained through the observations of Lillie. He found that in cattle, when the chorionic

In birds the activity of the gonads likewise controls to a large extent the development of secondary sexual characteristics.

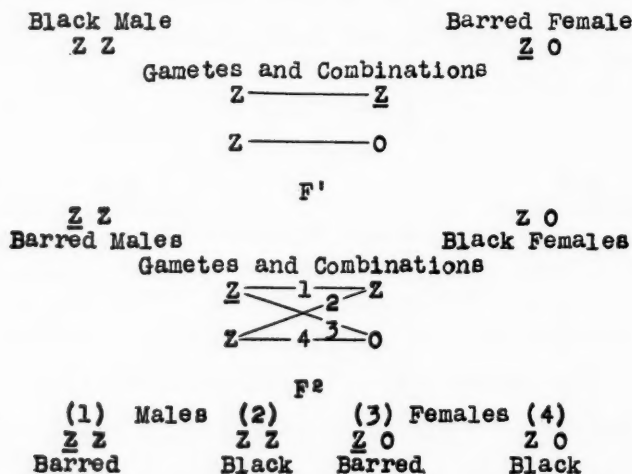


FIG. 8. DIAGRAM SHOWING CROSS RECIPROCAL TO THAT SHOWN IN FIGURE 7

This has been nicely demonstrated by Goodale and Morgan in castration and transplantation experiments on ducks and fowls. Most striking is the case of female birds, which, when castrated while still young, develop the male plumage and posture.

The whole problem of sex hormones is very complicated, for it has been shown that the secretion of the gonads is merely one link in the chain of factors, and that other endocrine glands contribute to form a complex of factors, which controls to a large extent the expression of the genes for the secondary sexual

characteristics. In the development of sex in vertebrates, the genes for the production of sex-hormones are probably second only in their importance and in their evolution to those genes which determine whether ova or sperm shall be formed in an individual.

It has been clearly demonstrated that the genes for the secondary sexual characteristics lie in the autosomes and therefore each sex has also a double set of those for the opposite sex. The expression of one set or the other will depend on the sex genes. Thus for example in cases where the male is heterogametic, the presence of a single X-chromosome in all the cells of the individual, together with the normal secretion of the male gonads, causes the male genes for the secondary sexual characteristics to develop. By castration and transplantation of ovaries into an immature individual, the normal condition may be upset, and the female secondary sex genes brought into action, as in Steinach's feminized rats.

It has been well demonstrated in insects that castration even of very young individuals produces no effect upon the secondary sexual characteristics when the animal reaches its adult form. Even the implantation of gonads of the opposite sex results in no change. The growth and development of the soma seems fixed by its chromosomal complex and not alterable by any sex-hormone. This rigidity of sexual development in insects may be coupled with the fact that normal hermaphroditism is extremely rare in this group.

Crustacea and insects, when parasitized, may show alterations of the secondary sexual characteristics, especially in the case of the males which then appear externally like females. In the Crustacea the best case is perhaps that of *Inachus*, described by Smith. The parasitized male becomes similar to the normal female in the form of its claw, abdomen, and abdominal appendages. Among insects *Thelia bimaculata*, described by the author, is a most striking example. Parasitized males resemble females even to the minute structure of the chitinous integument. Such alterations are most likely due to an entire upset of the metabolism of the host and the internal environment is such

that the genes for the male secondary sexual characteristics fail to find the necessary conditions for their expression in the developing soma.

7. GYNANDROMORPHS AND MOSAICS

In insects and crustacea there occasionally appear abnormal individuals which are mixtures of male and female individuals. Sometimes the demarcation is exactly median, one half being male, and the other half female. These are true gynandromorphs. There are, however, cases where the division is dorso-ventral or antero-posterior, and again the individual may be a "patch-quilt" of male and female parts, these latter being mosaics or intersex individuals such as described for moths by Goldschmidt and for daphnids by Banta.

Insect gynandromorphs do not necessarily have the gonad of the corresponding sex in their respective halves, showing that the soma is not moulded by sex hormones. The cause of gynandromorphism was studied by Boveri and also by Morgan. Boveri claimed for gynandromorph bees of crossed races that the male half was maternal, and the female half hybrid. If after the division of the egg nucleus a sperm united with one of the two daughter nuclei, that half would be female, whereas the sister nucleus developing parthenogenetically would form a male half which would be purely maternal. This explanation holds good for some cases, but Morgan finds in *Drosophila* that the male portions often bear paternal characteristics due to genes lying in chromosomes other than the X-chromosome. He, therefore, concludes that at times an X-chromosome is lost in the mitosis of a (female) zygote, and the nucleus which fails to get two X-chromosomes develops into the male portion of the gynandromorph. A misplaced X-chromosome in a primary germ cell may cause testes to form in a female. Such a case was found in *Thelia* where an actual chromosome count proved an X-chromosome to be missing in all the countable metaphase plates. The soma of the individual was purely female, however.

It is rather difficult to offer any simple mechanical explanation for the mosaics or sex intergrades of moths and daphnids. Gold-

schmidt has attempted to explain his results upon a quantitative basis, assigning values for the determiners for maleness and femaleness together with the postulation that the strength of these determiners varies in different races. Thus, the crossing of a strong male race with weak male races brings about an upset of the normal conditions and establishes a balance of factors where neither one sex nor the other predominates, and thus we get the expression of two sets of genes in various parts of the organism. Bridges' recent work on intersex forms in triploid races of *Drosophila* would indicate that where the normal relation of sex genes (located in the X-chromosome) to the autosomal genes is upset, either by a preponderance of one or the other, then sex abnormalities of many sorts may be expected.

8. HERMAPHRODITISM

One of the most obscure problems of the entire sex question is that of hermaphroditism, the production of ova and sperm by a single individual. This condition is found normally in many groups of invertebrates: coelenterates, ctenophores, flat worms, round worms, annelids, molluscs, and some crustacea. It is, however, the exception rather than the rule and must be viewed as a modification of the bisexual condition necessitated to insure insemination in animals of a less gregarious nature. Sometimes hermaphrodites are female in form, and again they resemble more closely males of the group to which they belong. In certain nematodes, as in *Rhabdites aberrans*, an occasional male is found among thousands of hermaphrodites of female form. Miss Krüger has shown that occasionally there is the failure of one chromosome to become incorporated in one of the second spermatocytes. Spermatozoa resulting from such deficient spermatocytes may be the cause of those occasional zygotes which result in males. Boveri and Schleip have shown that in the case of *Angiostomum*, a nematode in which hermaphroditic individuals give rise to a sexual generation, male-determining sperm are formed through the failure of one-half of the spermatids to include the X-chromosome. Since our knowledge of the chromo-

somes in hermaphroditism is scant, it is hardly worth while at present to speculate on the mechanism which produces such individuals.

That the sexual tendencies of hermaphroditic forms is often in a sensitive balance, influenced by external conditions, is shown by the experiments of Baltzer on *Bonellia* and Gould on *Crepidula*. In *Bonellia* there are produced minute motile larvae with hermaphroditic potentialities. If the free swimming larvae find the proboscis of a female *Bonellia*, they attach themselves and develop into minute males after a parasitic existence of about four days. If, however, no proboscis is found, the motile larva sinks to the bottom and develops into a female. In this case we may say that probably some secretion from the proboscis of the female stimulates the development of the male anlage and that this is accompanied by the suppression of the female fundaments. Likewise the absence of the proboscis secretion allows the female fundaments to develop while those of the male are suppressed. Intermediates were produced by Baltzer by allowing larvae to attach to a proboscis and then removing them at intervals of less than four days. In *Crepidula plana*, a hermaphroditic gasteropod which is normally a protandric hermaphrodite, Gould has shown that the presence of older individuals in the female state of development causes the production of sperm in small individuals nearby. Isolated small individuals, however, omit sperm production and form ova. Here is an animal in sensitive balance influenced by a secretion which probably comes to it through the sea water. The problem of hermaphroditism, its mechanism and relationship to bisexual reproduction, is well worthy of intensive study. From such exceptions to the general rule we may hope to learn much about the normal mechanism of sex-determination.

9. CONCLUSION

Finally, one may ask can sex ever be controlled? There seem to be two avenues of approach. In forms in which the female is heterogametic, external conditions may control maturation

and thereby sex, as in the case of Seiler's moths and Riddle's pigeons. Where, however, the male is heterogametic, sex could be controlled only by an agency which would differentially aid or inhibit the progress of one of the two types of sperm in its approach to or penetration of the ovum. The way is not closed and the facts so far learned about sex-determination make it seem not at all unlikely that definite control of sex will be established for many organisms in years not far distant.

THE MEANDER PATTERNS OF RIOS SECURÉ AND MAMORÉ, EASTERN BOLIVIA¹

KIRTLEY F. MATHER

The greater part of northeastern Bolivia is a lowland plain drained by a network of streams which unite to form Rio Madeira, one of the larger tributaries to the Amazon. Between Guajara Mirim and Porto Velho (see fig. 1), the Madeira crosses the northwestern extremity of the Pre-Cambrian shield of Brazil² in a series of cataracts and rapids. The altitude of the river bed at the first of the cascades, close to Guajara Mirim, determines the level of the floor of the entire basin stretching from that point to the eastern foot of the Andes of Bolivia and Peru. The streams from the mountains debouch upon this lowland, heavily laden with silt, and the plain is in consequence a plain of aggradation. Its surface is between 600 and 1000 feet above sea level, and slopes with remarkable uniformity and exceedingly low gradient from the foot hills of the Andes to the head of the cataracts of the Madeira. Because of the uniformly low gradient the streams which traverse this featureless plain for hundreds of miles have developed meanders of unusual complexity and perfection. The opportunity which they afford for the study of old age stream patterns is excellent.

While engaged in geological explorations for Richmond Levering and Company in August and September, 1920, I crossed the eastern Andes from Cochabamba to the headwaters of Rio Chaparé, and travelled overland in the foothill region to Rio Securé.³ After a brief examination of the upper reaches of this

¹ A paper presented before the Section of Geology of the Ohio Academy of Science, April, 1922.

² Branner, J. C., Geol. Map of Brazil, Bull. Geol. Soc. of Amer., vol. 30, plate 7, 1919.

³ Mather, K. F., Explorations in the Land of the Yuracarés, Eastern Bolivia; Geographical Review, vol. 12, pp. 42-56, 1922.

river, I travelled as rapidly as possible to Trinidad, descending Rio Securé and Rio Mamoré. The journey gave me an oppor-

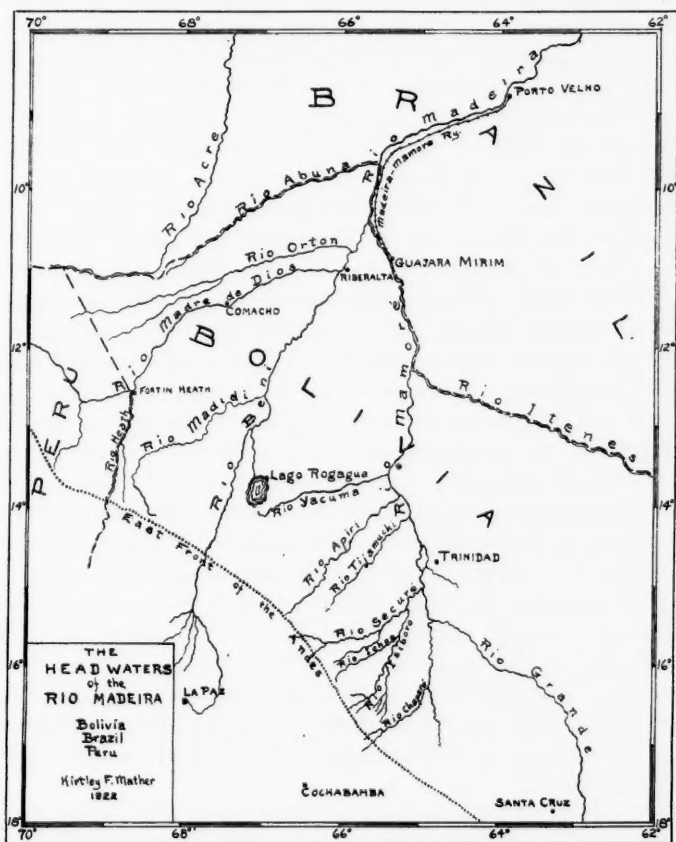


FIG. 1

tunity to map portions of the rivers and provided the data for this paper.

The exigencies of travel made the compilation of the map of secondary importance, and therefore the methods used in map-

ping were perforce such as would not delay progress. Transportation was by means of dugout canoes, propelled and piloted by Yuracarés Indians. Directions were determined by frequent readings of a Brunton compass; distances were approximated by noting the interval of time which elapsed while the canoe was on the determined bearing. The speed of the canoe had been previously ascertained by timing it over a marked course, and, although the methods used in making the map were obviously crude and subject to considerable error, it is believed that the results obtained in the main are fairly accurate.

Rio Securé, above the junction with Rio Isiboro at Puerto Calvimonte, averages a hundred yards in width. It is a brown, silt laden stream, sliding swiftly between banks of clay or sand, capped with six or eight feet of rich black soil, which rise abruptly from the water's edge to the level of the jungle covered plain. At low water these banks are 15 to 25 feet high, but in the rainy season the river brims its banks and floods the ground between the trees of the tropical jungle. The Isiboro is nearly as large as the Securé above the junction of the two. The Securé's volume is therefore nearly doubled at Puerto Calvimonte. From that point to its mouth the river averages a little over 150 yards in width. Rio Mamoré is a much larger stream, with a width of at least a quarter of a mile at low water, between the mouth of the Securé and the vicinity of Trinidad. A detailed map of the lower part of the Securé and a portion of the Mamoré forms figure 2. Throughout the area of this map and for many miles upstream and downstream beyond it, the gradient of the Securé and Mamoré is practically constant, less than half a foot per mile of river course.

The meander patterns of the rivers, shown in figure 2, are characteristic; curve follows curve in dizzy succession along the tortuous stream course. The typical meander curve is not an arc of a circle, but is formed of short sharp bends alternating with long, comparatively straight stretches. Many times while paddling steadily downstream we found ourselves within a hundred yards or so of the place where we had been an hour before. Occasionally we noted cut-offs where during the previous rainy

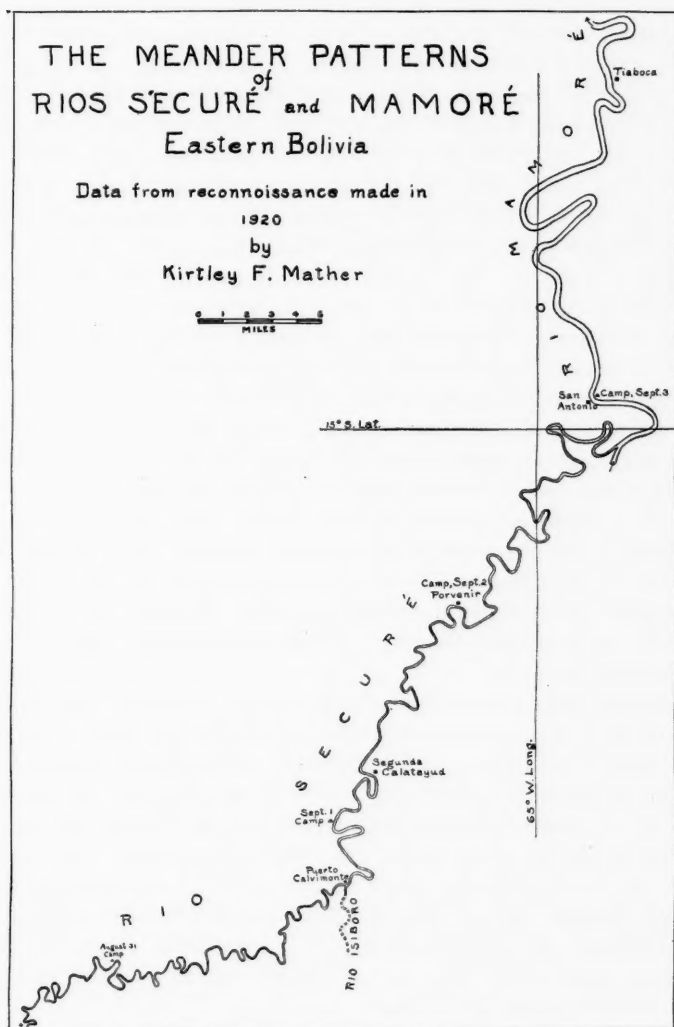


FIG. 2

season the stream had straightened its course and abandoned a long-used channel; elsewhere the river banks were reduced to a knife-edge by the close crowding of meander loops.

Apparently there is a definite correlation between the meander pattern and the volume of the stream; this conclusion is really the excuse for this brief note. Where the river volume is comparatively small, meander curves are numerous, close-crowded, and short. With increase in volume the curves become longer, more widely spaced, and fewer. Three distinctive patterns are clearly shown in figure 2. These correspond to the varied volume of the streams involved. The Securé above its junction with the Isiboro displays twice as many meander curves in a given distance as are found below Puerto Calvimonte, where its volume is nearly doubled by the accession of the Isiboro. Likewise the lower part of the Securé has many more meanders than has the Mamoré, much the larger of the two streams.

This change in meander pattern seems to be solely a response to the change in volume of the rivers. The gradient is not altered, nor is the current appreciably swifter. The change, as indicated by the map, involves a lengthening of the straight stretches between the short sharp curves. Possibly the greater inertia incident upon the larger volume is the major cause of the modification.

It is of interest to note that in this land, where transportation routes and lines of travel are restricted to the navigable waters, the untutored Indians are sufficiently adept physiographers to note this correlation between river volume and meander dimensions. Distances between *chacras*, the tiny clearings under cultivation along the river banks, are reported in terms of the numbers of "turns" in the river's course. Thus I was told that it would be five "turns" from the mouth of the Securé to the port of Trinidad; but that because the Mamoré was very wide the "turns" were very long, and it would require from sunrise to sunset to traverse the distance.

A little later in the same field season I had opportunity to check the conclusion, reached on the Securé and Mamoré, by similar observations on Rio Heath and its tributary, Rio Najegua,

on the frontier between northern Bolivia and eastern Peru (fig. 1). The Najegua is less than a third as large as the Securé, but its gradient is approximately the same. In harmony with its slight volume, its meander curves were very short, extremely close spaced, and numerous. Working upstream in it, at a pace of $2\frac{1}{2}$ miles per hour, it was necessary to take bearings every minute or two in order to get any results at all from the effort to map its tortuous course. Rio Heath, only slightly less in volume than the Securé, has a meander pattern practically identical with that of the Securé above Puerto Calvimonte.

PRIMITIVE MUSICAL INSTRUMENTS OF THE DENISON COLLECTION

KARL H. ESCHMAN

The collection of primitive musical instruments at present located in the building of the Conservatory of Music, Denison University, although small in number, includes all the main types of instrumental evolution. It is the result of miscellaneous gifts of alumni from mission fields. The fact that this collection so completely illustrates a brief outline of the subject, it is thought, should encourage other colleges with departments of music, to begin collections of like character.¹ In addition, it is hoped that a description of some of the specimens may be of interest to students of the subject.

With the aid of certain ethnological principles, and by methods not unlike those used in the classification by distribution, of fossil remains in strata of different periods, an order of evolution of musical instruments has been formulated, which may be accepted in general. In determining the priority of instrumental types, we are hindered by the nature of the materials themselves. However, by collecting instruments from tribes which represent all stages of civilization existing at present, we can secure, of course, illustrations of many periods of construction. It is this fact which adds to the interest of any collection, whatever the age of the particular instruments themselves. There have been two opposing theories of priority: one starting with the percussion type, and the other favoring the pipe or horn type. Both types are so simple as to need little ingenuity for construction. Handclapping would easily lead to the beating of objects together, and shouting through the hands would be followed by

¹ The splendid collections at the University of Michigan, Yale, and Pennsylvania, as well as that at the Metropolitan Museum, New York, are based upon the gift of a single large private collection.

the use of a crudely rolled horn, while natural whistles literally grow on bushes wherever reeds and bamboo are found.

The weight of authority, however, is with the former theory, as is also the evidence of ethnology. In fact, all seems to point to the following arrangement, which also coincides with relative difficulty of manufacture and complexity of idea:²

- I. Indefinite percussion
- II. Wind instruments—pipe type
- III. Wind instruments—horn type
- IV. Definite percussion
- V. Stringed instruments—without fingerboard
- VI. Stringed instruments—with fingerboard
- VII. Stringed instruments—with bow, without and with fingerboard
- VIII. Multipipes—organ type.

I. INDEFINITE PERCUSSION

1. Ngoma (war drum)—*Africa*. This most primitive type of drum is a section cut from a tree-trunk. Hollow trees are still occasionally used as drums, and the attempt to make such stationary instruments portable, probably produced the first drum of this character. This drum is 96.8 cm. in length by 34 cm. in diameter at the largest end. The body is cut down by a sudden shoulder to a diameter of 12.5 cm. at the smaller end. The drum is crudely hollowed out, and this small end has an opening 8 cm. in diameter, surrounded by a tin collar but with no leather head. This narrowing, and the small opening, even without a head, greatly aids the sonority. The rawhide head at the larger end is fastened to the drum by three rows of wooden pegs. Two sets of three wooden projections and one of two, were left on the drum when carved, to be used as handles or for thongs.

2. Ndunga—*Africa*. This drum is 304 cm. (9 feet 8 inches) in length, and is interesting as one of the few drums of this type in American collections. Drums of still larger size are made by the natives. This tree-trunk has been trimmed with greater care than the Ngoma above, to 26.5 cm. diameter at the large end and 12 cm. at the smaller. Both ends are covered with hide and are strung together by ten thongs of rawhide with hair

² This outline has been simplified for use with illustrations selected.

attached, running the entire length of the drum. It is carried by four men, two on each side of a long handle which is carved from the body of the tree. The drum as well as the drum-stock (32 cm. long, 2 cm. diameter) which is not padded, is painted in alternate red and black circles.

3. Drum—*Africa*. A well made cylinder, 49.5 cm. in length, 26 cm. in diameter, has two heads laced together by a very intricate network of rattan which covers the entire drum. The whole drum evidences much more skill of workmanship than the preceding, and produces a very satisfactory tone, as the tight lacing greatly increases the resonance.

4. Ozee (stationary drum)—*Burma*. This drum is made of wood in the shape of a goblet 38 cm. high and 15.5 cm. in diameter, lacquered black and red. The head is painted with a smaller circle of black and is fastened by thongs to a wire at the base of the head. The wooden base of this drum is hollow. A companion drum of the same general size and finish has a skin on each end and a thong which slips around the neck, making it possible to play with the fists while moving about.

II. WIND INSTRUMENTS—PIPE. TYPE

5. Siakuhachi—*Japan*. This direct flute is made from a thick bamboo stem, using the natural swell of the reed. It is blown at one end where a piece is cut off to afford a position for the lip. The length is 49 cm. and the diameter 1.7 cm. swelling to 2.3 cm. There are four finger-holes in the front and one in the back, while other smaller subdivisions of pitch are obtained by only partly closing these holes with the fingers. There is a distinct pattern for this type so that the distance from joint to joint of the bamboo averages 17, 14 and 8.5 cm. respectively. This specimen measures 18, 14 and 9 cm.

6. Traverse flute—*Burma*. This flute is lacquered black and has a ring of ivory at each end; 40.5 cm. long, 2 cm. diameter. Six holes for fingering and one for blowing.

7. Ti or Yuēh—*China*. Seven holes in front and one in back of pipe. The mouth-hole is divided by a small partition into two parts. Made of bamboo, 28 cm. long, 1.5 cm. diameter.

8. Fife—*Garó*. Traverse; very small bore; reed 55 cm. long, 1.1 cm. inside diameter. The finger holes are near the opposite end from the mouth-hole.

III. WIND INSTRUMENTS—HORN TYPE

9. Wooden trumpet—*Africa*. Total length, 87 cm. In this horn the mouthpiece is on the side, and the actual blowing length is 58 cm. The diameter at the large end is 9 cm. From the mouthpiece to the open end, the horn is covered with natural fibre and wrapped with rattan.

IV. DEFINITE PERCUSSION

10. Gong—*Burma*. Diameter 18 cm. with a 3 cm. edge turned up; but slight attempt at decoration.

11. Kyizi—*Burma*. Two very small hollow hemispheres of bronze through which a string is fastened, are allowed to strike together, giving the impression of tinkling bells. These are only 3 cm. across.

12. Zanze or Biti—*Africa*. Eleven tongues of iron are mounted on a hollow sound board in such fashion that they can be plucked by the thumbs when the instrument is held in the two hands. This instrument is akin to the marimbas but scarcely a typical percussion type. According to the savage notion, the twanging is made more beautiful by the rattling of small beads on some of the tongues, when the instrument is played. The box is 27.5 cm. by 13 and 16 cm. (flaring) and 1.5 to 3.5 cm. deep. The vibration of the other end of each tongue is stopped by a strip of leather on the face of the instrument. The scales of no two instruments of this type are alike. The Denison specimen gives: g' flat, f' , c' , a' , B, A flat, A, d flat, f , b , e' .

V. STRINGED INSTRUMENTS—WITHOUT FINGERBOARD

13. Gopi-Jantra, Monochord—*Garó*. (Tura, Assam.) A calabash gourd is fitted with a skin bottom through which a single wire is fastened by means of a button. (This use of a European

button is thought highly ornamental.) A piece of bamboo is split part way and fastened to the sides of the gourd, and to this, the wire is stretched by means of a single peg in the side. Total height 78 cm.; diameter of body, 18 cm.; very primitive. The pitch is changed by pressing in on the bamboo strips while the tone is sounded.

14. Ichigenkin or Sumagota (monochord)—*Japan*. The one string is stretched over a board of cherry-wood 110 cm. long and 10.5 cm. wide. The supporting ivory bridge is missing in this specimen. The string is tuned to $f\sharp$ of our scale—a note which may be considered the principal note of the Japanese tonal-system. All Japanese instruments are elaborately decorated. This one has a circular piece of embroidery near the end, and is suspended by a red and yellow cord from the other end when not in use. When played, it is laid horizontal on a low table. The instrument has no fingerboard, but the pitch is changed by an ivory cylinder worn on the second finger of the left hand which is pressed against the string to furnish nodes for the different notes. The ivory spots or designs found on some instruments to indicate these points, are not present in this specimen.

VI. STRINGED INSTRUMENTS WITH FINGERBOARDS

Samisen—*Japan*. This instrument has a fingerboard but no frets. It is related to the Chinese Sanheen, each having three strings and a long neck. The body of the Sanheen is round and of the Samisen rectangular, in this case 20 cm. by 18 cm., 10.5 cm. thick, covered with catskin. The length of the entire instrument is 94 cm. The three strings are turned in three ways:— $c'\sharp$, $f'\sharp$, $c''\sharp$; $c'\sharp$, $g'\sharp$, $c''\sharp$; and $g'\sharp$, $c''\sharp$, $f''\sharp$. The Samisen is played with a large wooded pick over 20 cm. long, the strings being struck below where the neck joins the body. The face is strengthened there with a small extra piece of parchment which receives the blow of the pick, thus producing two sounds, the plucking of the strings and the stroke on the body.

16. Yueh Ch'in (Moon guitar)—*China*. This instrument derives its name from its round shape, 33.5 cm. in diameter, and 3.5 cm. thick, both surfaces being flat. It is the first string

instrument on our list which gives in its construction, information as to actual scale relationships. There are eleven very high wooden frets, eight on the body and three on the neck. The top one serves as a bridge and the frets decrease in height all the way down. The four strings are tuned in pairs, and are often plucked with the finger nails which are grown conveniently long. A loose wire fastened inside the body jangles when the instrument is played, and adds to the effect, somewhat as the beads do in the African zanze.

17. Gekkin (Moon guitar)—*Japan*. A comparison with no. 16 shows the intimate connection between China and Japan. The Japanese instruments always show much more care in construction and beauty of ornament than the parallel type in China. The sizes of the two instruments are almost identical (the body of the Gekkin is 34 cm. diameter, by 3.5 cm.) but the number and locations of the frets are different. The Gekkin has nine in all, four on the body and five on the neck. The frets are of ivory. Carved wooden ornaments are located about where sound-holes might be expected on a medieval viol. A snake skin protects the face of the instrument from the blows of the small pick. This instrument also contains a snare.

VII. STRINGED INSTRUMENTS WITH BOW

18. Mendicant's fiddle—*Thibet* (Darjiling). This instrument is a crude Thibetan counterpart of the Chinese urheen (19) and in every way shows its low origin. There is only the slightest attempt at decoration with inaccurate cross-markings on the neck. The tuning-pegs are not mates, but evidently have been picked up somewhere, and put to this use. The two "strings" are simple bunches of about a dozen horse-hairs each, like those on the bow. The evolution of bows is in itself an interesting subject. This bow is most primitive, being simply a bent stick, but there is a notch at one end which makes it possible to loosen the hair when not in use. A peculiar feature of this instrument (as of no. 19) is that the hair of the bow passes between the strings so that the bow cannot be removed from the strings. The body of the instrument, which corresponds in position to the

head of a mallet, is a section of bamboo 10 cm. in diameter and 13 cm. long. The skin head is fastened on with wooden pegs which project irregularly.

19. Urheen—*China*. This type is one of the oldest Chinese stringed instruments. Although this specimen shows great care in construction, having inlaid pegs and top, it is almost as primitive as no. 18, because the hair of the bow passes between the strings; and, as the strings are too far from the neck to be stopped, only one combination of tone is possible. The improvement over no. 18 is mainly in the strings themselves, which can be tuned to $f\sharp$ and $c\sharp$. The rasping sound of this open fifth is the only musical effect of this instrument. The bow is an advance, having something of the contour of a modern violin bow, but it does not seem to have been given the care bestowed on the instrument itself. The cylindrical body 11.5 cm. long by 8 cm. diameter, is made of wood covered with a snake-skin head.

20. Fiddle—*Thibet*. The body of this fiddle is made from a cocoanut shell, with a skin head fastened down over half the surface of the shell. A bundle of horse-hairs is stretched from the head to a peg in the handle. The wooden bridge is not fixed to the face of the head but is tied to the neck of the instrument by a string, and placed in position only when the hair is tightened. The hair of the bow does not pass between the hair of the string in this case. An interesting feature of this instrument is the fact that the maker has used part of an old flute for the neck, placing the mouth hole near the head and leaving four finger holes at the other end, into one of which the peg is placed. This use of old material at hand is characteristic although unexpected. Personal and tribal traits of this sort add interest to any collection of primitive instruments.

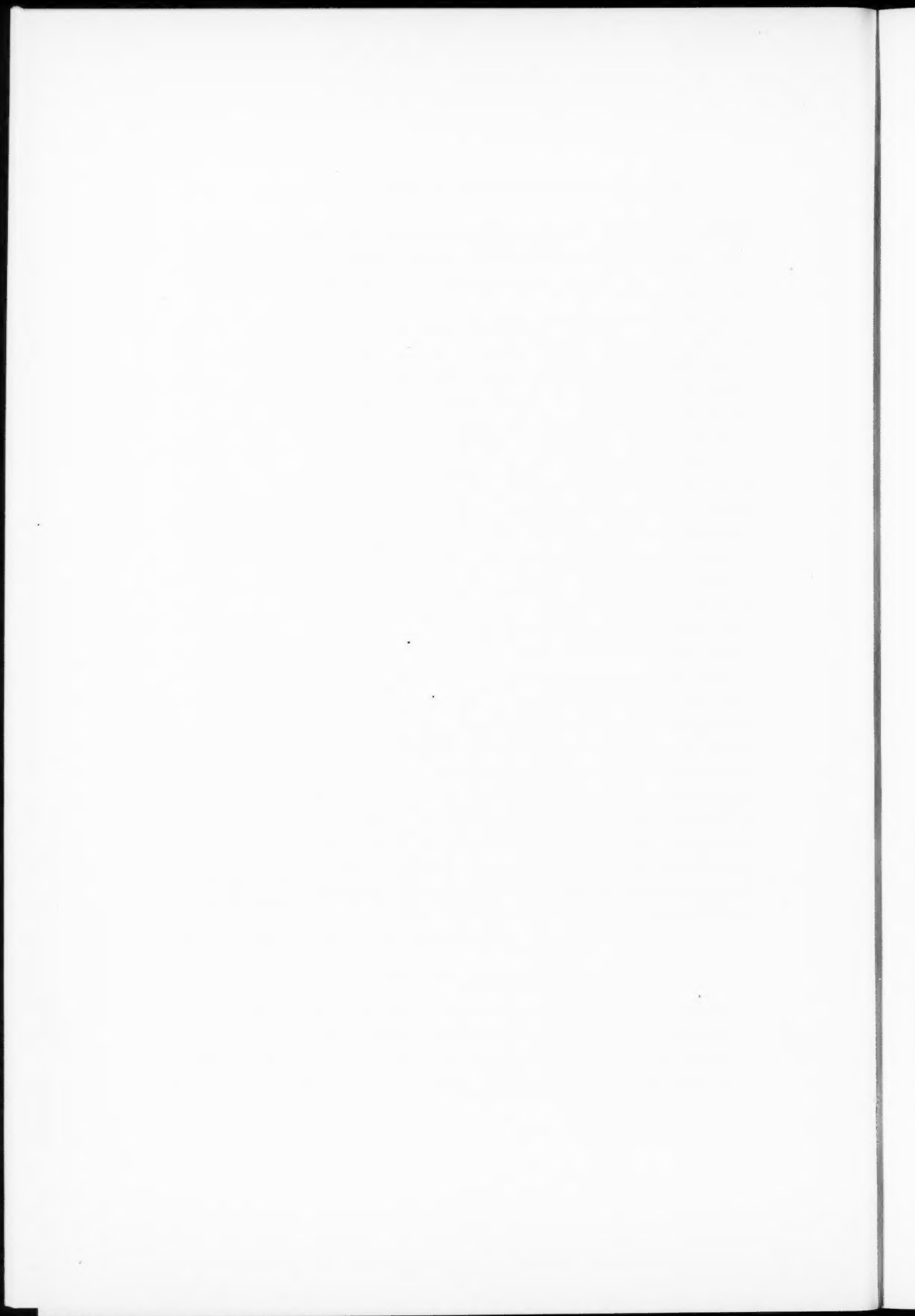
VIII. MULTIPIPES—ORGAN TYPE

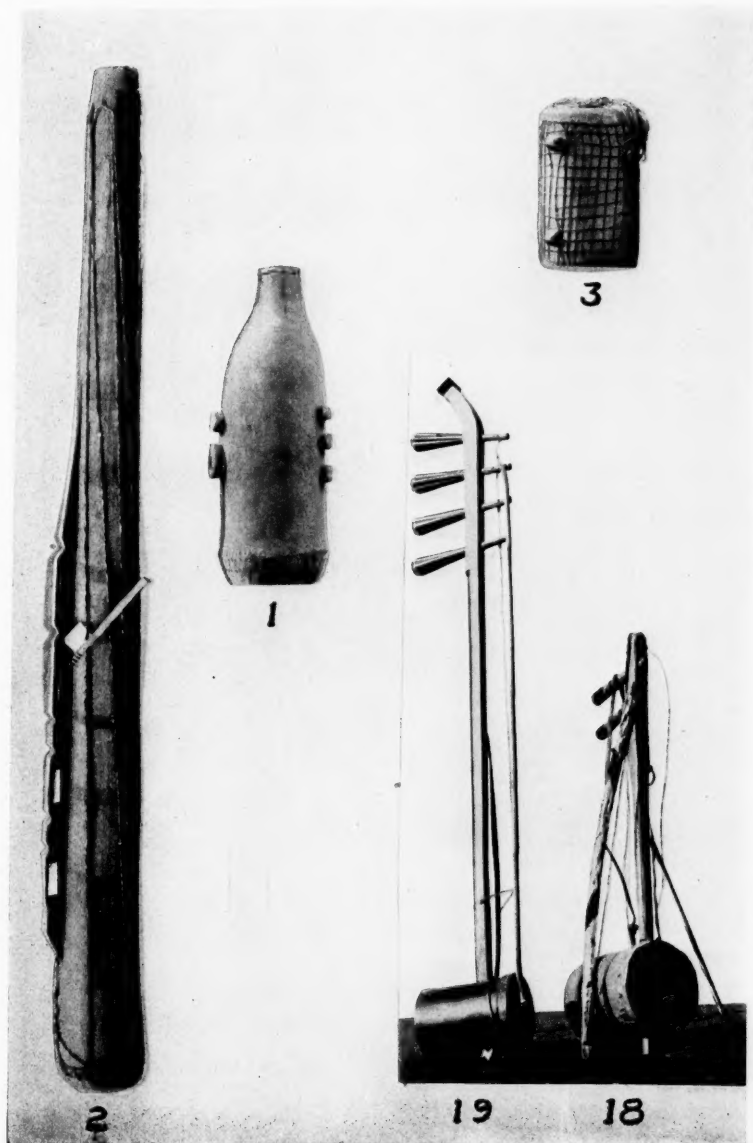
21. Muhso flute.—*Burma*. A reservoir made from a calabash gourd has five open pipes. The open pipes make possible a second tone from each pipe, by closing the lower holes which open on the bottom of the gourd. Because of the difficulty of

holding more than two pipes in the mouth, a substitute reservoir was sought. In some sections a hollow lump of clay is used, into which the pipes are fastened. No. 22 shows a further advance.

22. Sheng—*China*. Seventeen reeds of small bore are set in a lacquered cup of cherry-wood. The mouthpiece in primitive instruments was a long spout like that of the Muhso flute above, but it is now a much shorter projection covered with an ivory plate. Each of the pipes contains a very small free reed of copper, set level with the frame. The instrument is played by inspiration—i.e., by drawing in the breath—as otherwise moisture might settle on the reeds and affect the pitch. There are many interesting features connected with this instrument—the use of two mute pipes and the curious arrangement of pipes which gives it the Chinese name of “Bird-on-the-nest,” the fact that sounding length of the pipes is different from the apparent length, and the use of a free reed at such an early date. (The type is thought to be at least three thousand years old.)

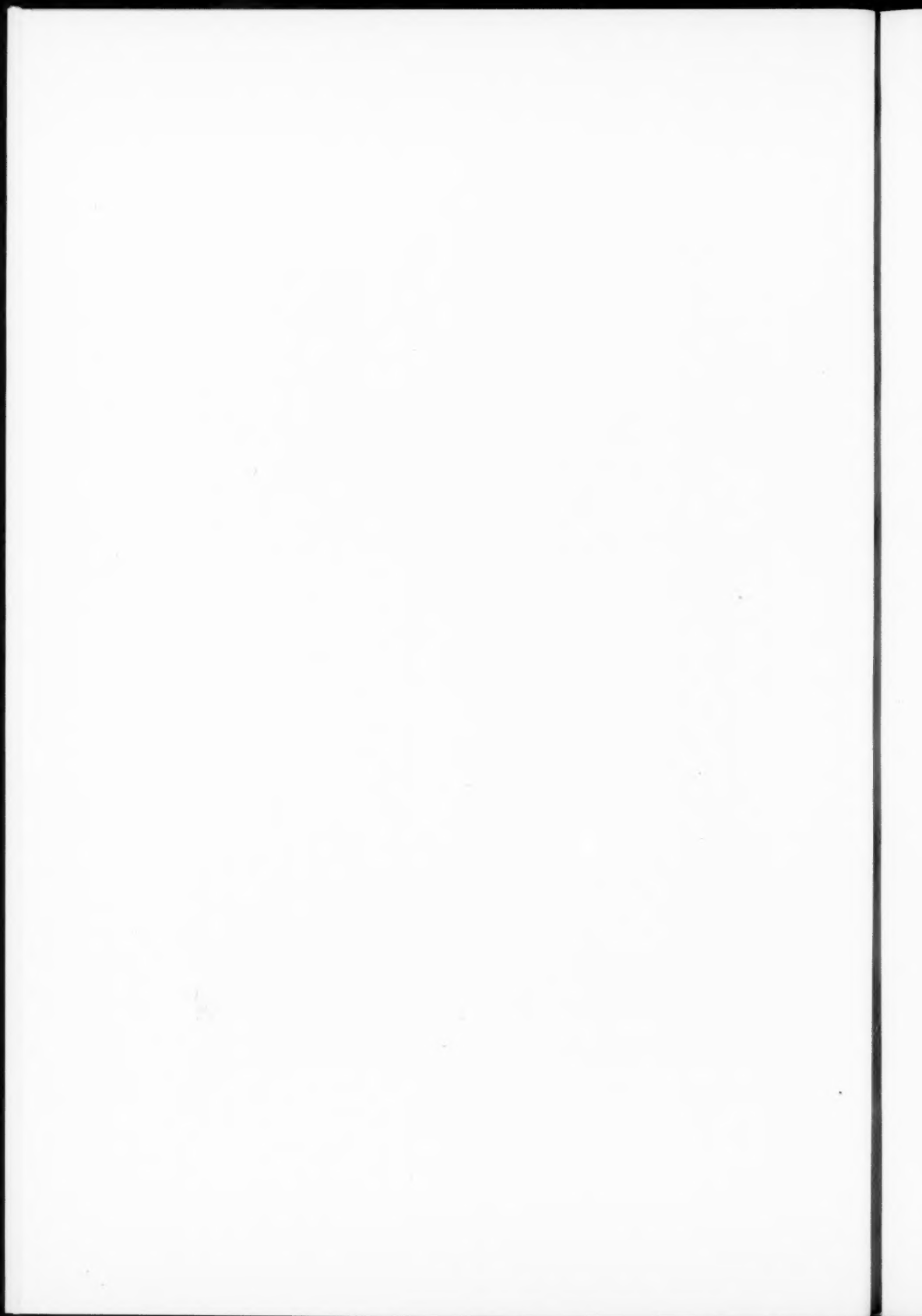
From the standpoint of the theory of scales there is the question of a mechanical origin of the sheng scale procured by the successive halving of differences, starting with the longest pipe, which is just the length of the Chinese foot. Further, the duplication of two notes of $f\sharp$ and $g\sharp$ by the use of four pipes, suggests an attempt at equal temperament—i.e., the production of true fourths with the upper and lower c sharps. The only difference in the scale of the Denison sheng from the normal type is that pipe no. 7 (counting from the left of the opening) gives c'' and pipe no. 11 gives c''' while in the usual instrument these are reversed.

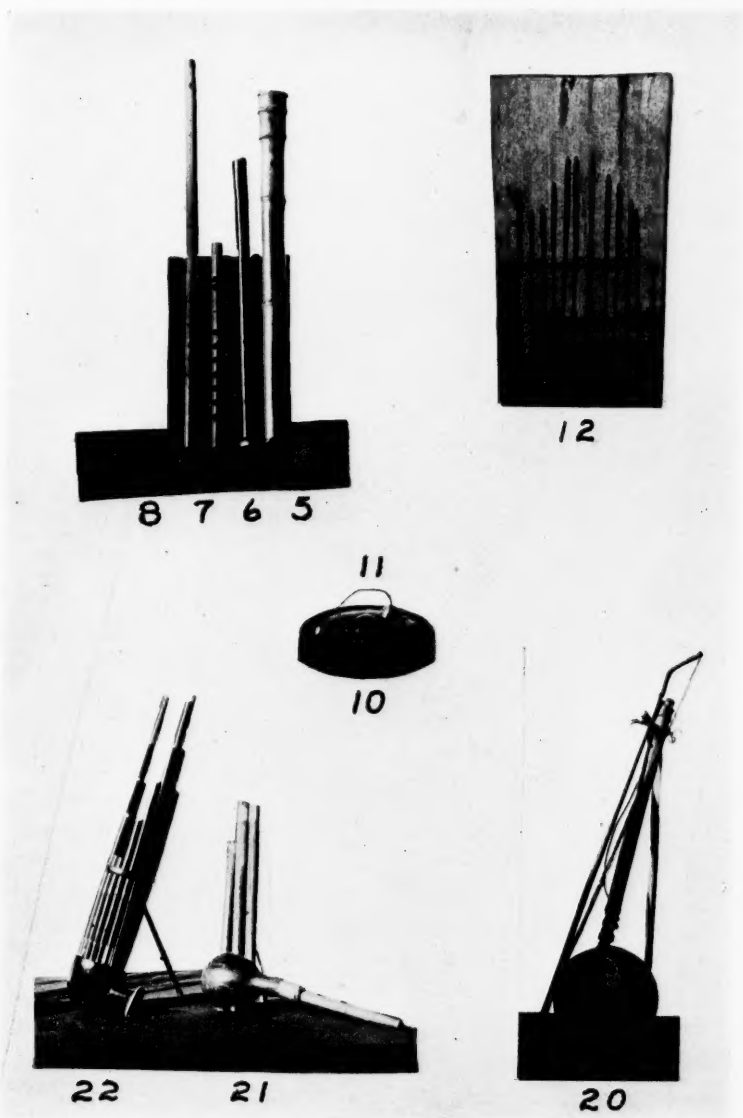




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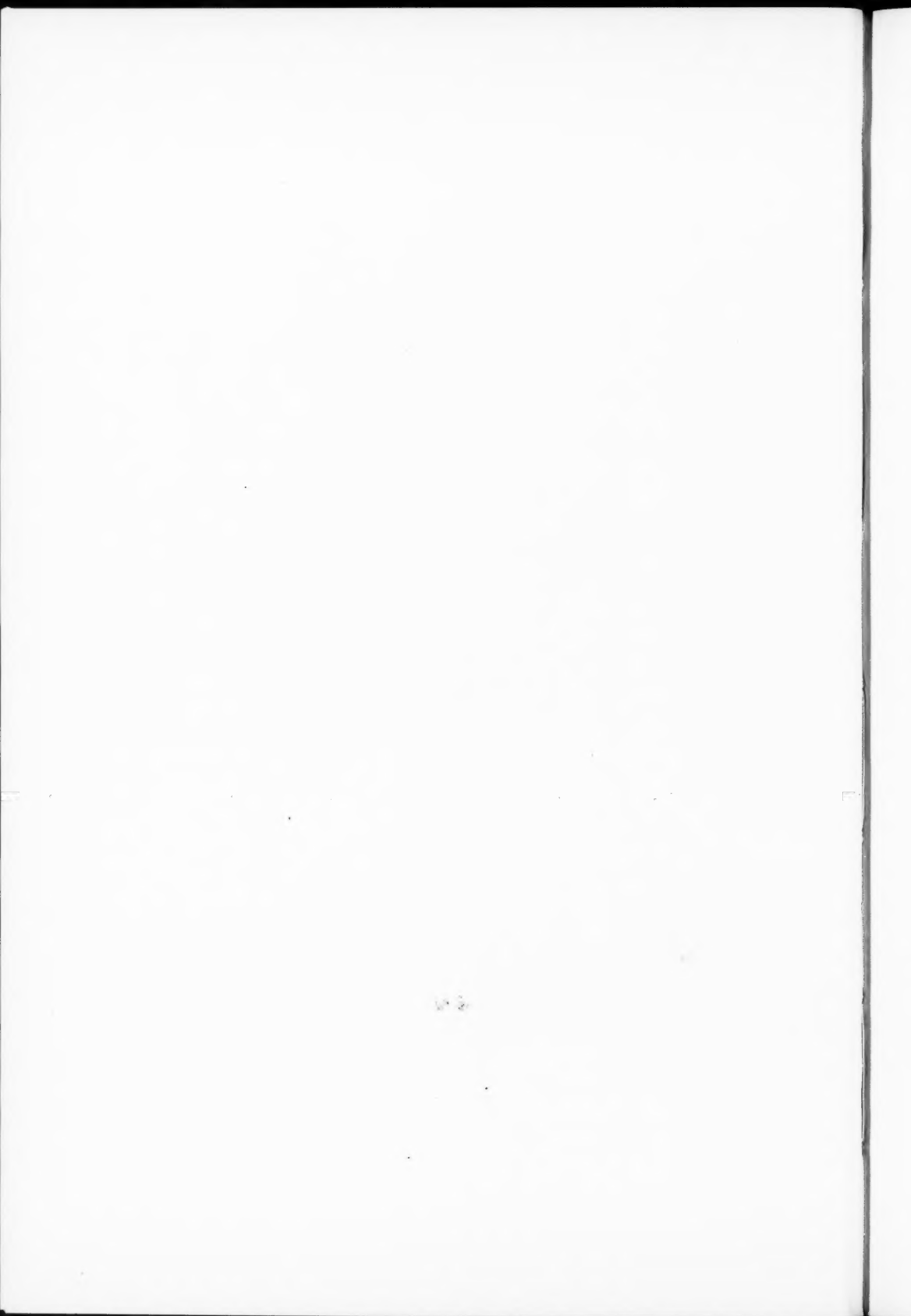
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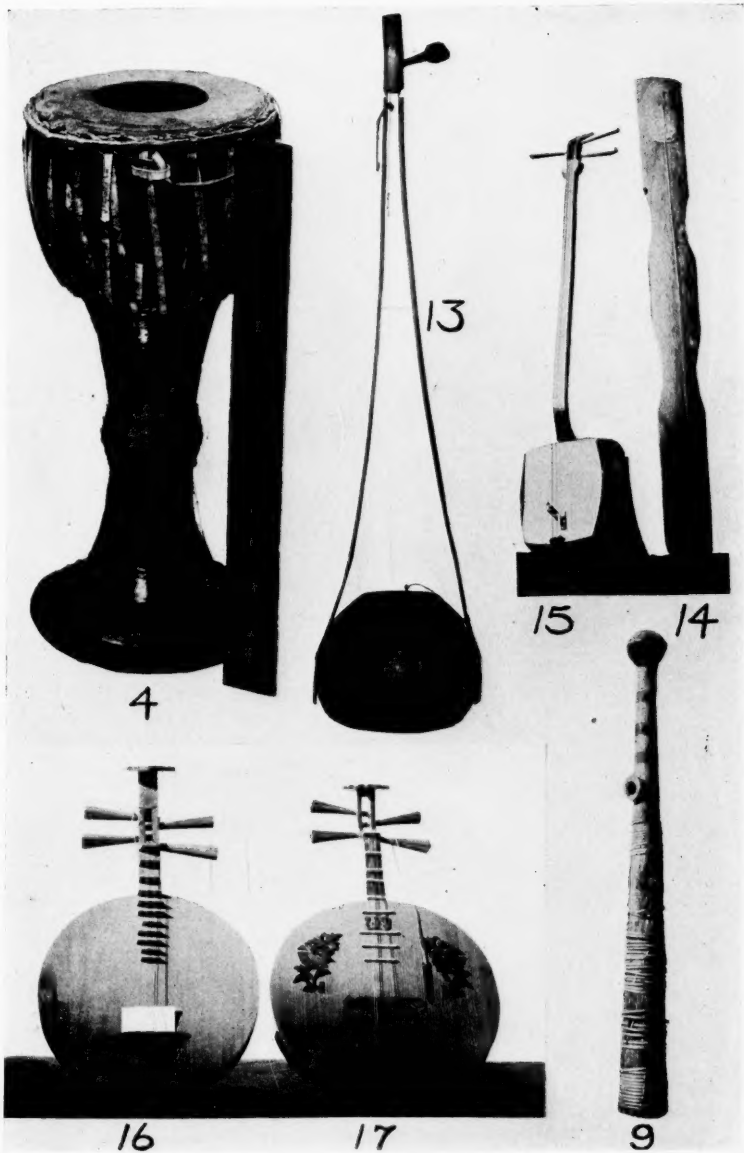




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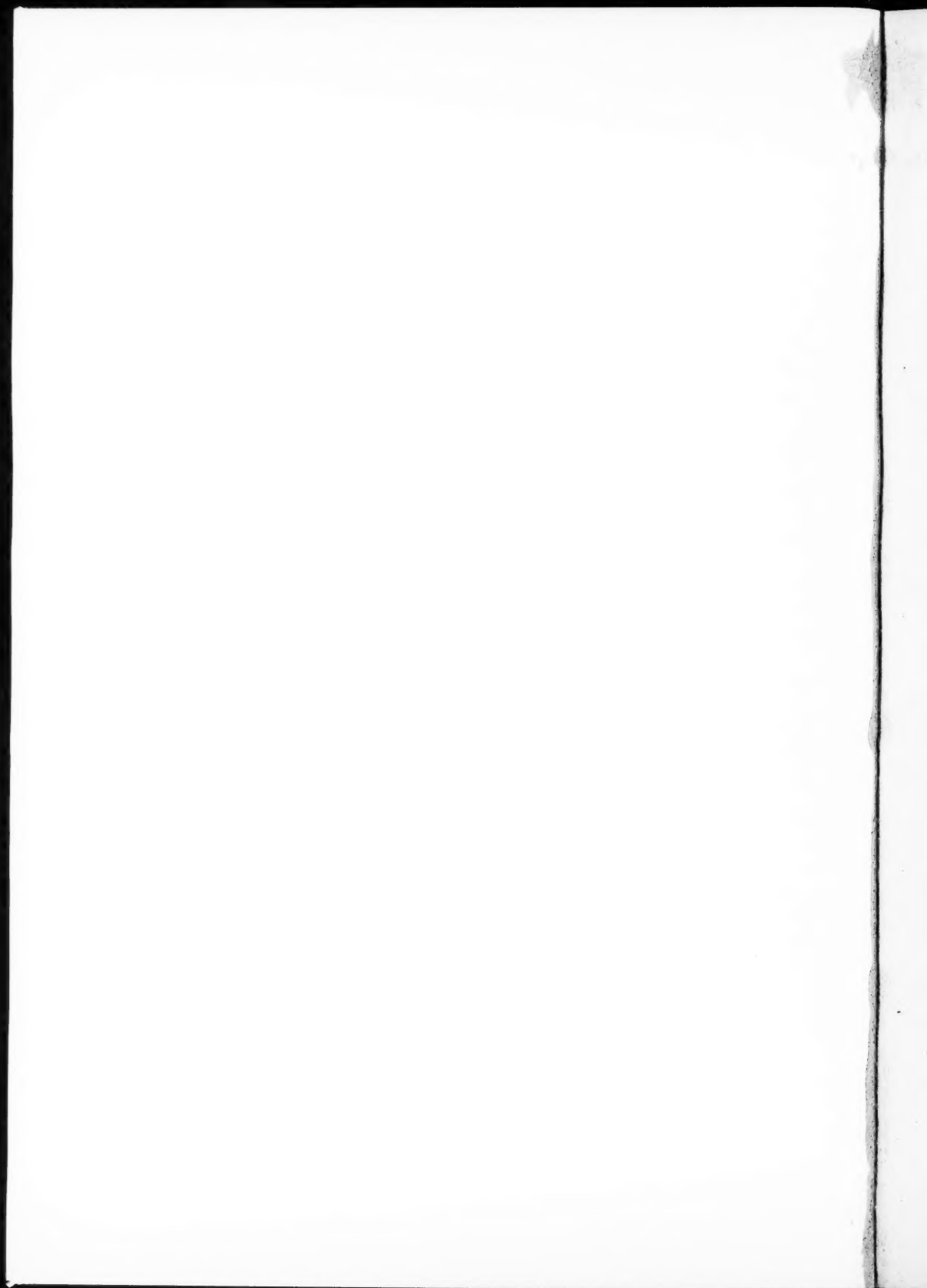
MUSICAL INSTRUMENTS





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MUSICAL INSTRUMENTS



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